DEPARTMENT OF BIOLOGY

MASTER OF SCIENCE DEGREE IN CONSERVATION AND EVOLUTION

Suckling behaviour of Apennine chamois: effects of pasture quality

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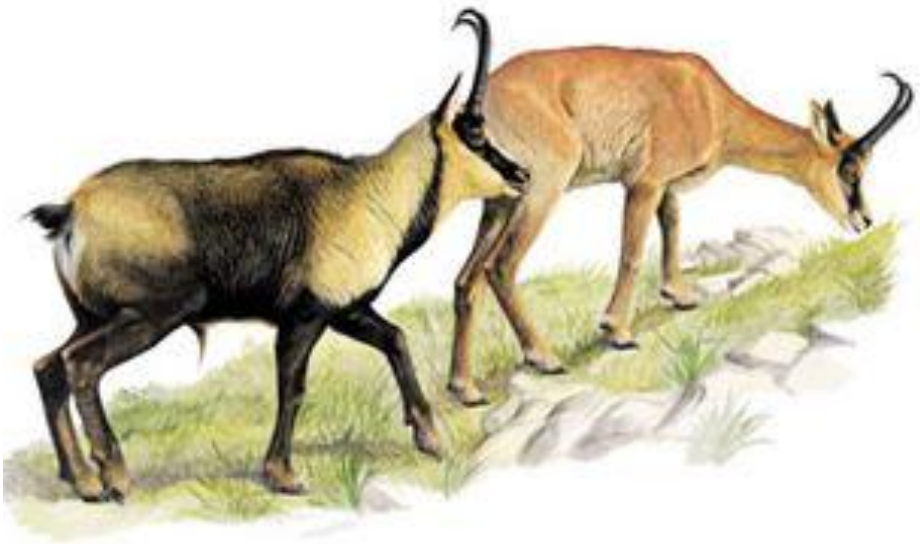
"…Call to mind from whence ye sprang:
'Ye were not form'd to live the life of brutes,
'But virtue to pursue and knowledge high."

"… Considerate la vostra semenza:
fatti non foste a viver come bruti,
ma per seguir virtute e conoscenza."

Dante Alighieri "The Divine Comedy"
(Canto XXVI, Ulysses' Last Voyage, vv. 112-120)
Translation of Henry Francis Cary



Abstract

Availability and quality of summer pasture influence body conditions of female ungulates and, in turn, the amount of maternal cares they provide to offspring. The intensity of maternal cares is strongly associated to winter survival of offspring, which is a key determinant of population dynamics of ungulates. Climate changes and the presence of competitors may affect the nutritional quality of summer forage for ungulates, reducing survival of offspring, but relevant information is very scarce in literature. I have evaluated the effects of pasture quality and competition with red deer *Cervus elaphus* on suckling behaviour and winter survival of Apennine chamois *Rupicapra pyrenaica ornata* kids in Abruzzo, Lazio and Molise National Park. Previous studies showed a high spatial/diet overlap between chamois and re-introduced red deer, with negative effects of the latter on pastures/diet quality and feeding intensity of female chamois. Through pellet group counts and behavioural observations, I compared suckling behaviour of chamois, as well as winter survival of chamois kids across three sites with different deer density and pasture quality (July-October 2013-2014, Sites A-B: deer present at high density; "poor" pasture; Site C: deer absent; "rich" pasture). My results have showed (*i*) a lower probability of suckling success, (*ii*) a lower suckling frequency and duration, (*iii*) a greater frequency of suckling attempts, (*iv*) a lower winter survival of chamois kids, in deer-present "poor" Sites than in the deer-free-rich one. These results suggested that frequency and intensity of maternal cares were the greatest in the area, where the quality of pasture and diet of female chamois during summer was the highest one. The current Climate change is expected to affect availability of nutritious, cold-adapted plant species for chamois, with resource exploitation by red deer further

depleting pasture. Both these factors are expected to affect the present and future conservation status of Apennine chamois.

Riassunto

La disponibilità di pascolo estivo di alta qualità influenza fortemente le condizioni fisiche delle femmine degli Ungulati e le cure materne che esse forniscono ai piccoli. A sua volta, questo influenza la sopravvivenza invernale dei piccoli, che è un fattore chiave per la dinamica di popolazione degli Ungulati. La qualità del pascolo potrebbe essere alterata dai cambiamenti ambientali e dalla presenza di un competitore, con effetti negativi sulla sopravvivenza degli Ungulati, ma studi al riguardo sono scarsi.

In questo lavoro ho valutato gli effetti della qualità del pascolo e della competizione col cervo rosso *Cervus elaphus* sul comportamento di allattamento e sulla sopravvivenza dei piccoli del camoscio appenninico *Rupicapra pyrenaica ornata* nel Parco Nazionale d'Abruzzo, Lazio e Molise. Studi precedenti hanno mostrato una elevata sovrapposizione spaziale/alimentare tra camoscio e cervo, con effetti negativi sulla qualità del pascolo e dell'alimentazione, oltre che sull'intensità di pascolo, in estate, delle femmine di camoscio. Mediante conteggio dei gruppi di escrementi e osservazioni comportamentali, ho confrontato il comportamento di allattamento e la sopravvivenza dei camoscetti tra tre siti con diversa densità di cervo e qualità del pascolo (Luglio-Ottobre 2013-2014, Siti A-B: pascolo impoverito, cervo presente ad alta densità; Sito C: pascolo nutriente, cervo assente). I risultati hanno mostrato (*i*) una maggiore probabilità di successo di poppata, (*ii*) frequenza e durata delle poppate maggiori; (*iii*) una frequenza di richieste di poppata minore, (*iv*) indici di sopravvivenza invernale dei camoscetti più alti nel sito non utilizzato dal cervo. Questi risultati suggeriscono che la frequenza e intensità delle cure materne sono state più alte nell'Area caratterizzata dal pascolo più ricco, non usata dal cervo, dove la qualità dell'alimentazione

delle femmine di camoscio è più alta. Molto probabilmente, il cambiamento climatico sta riducendo la disponibilità di specie vegetali nutrienti per il camoscio, adattate ai climi freddi, mentre l'azione del cervo accelera l'impoverimento del pascolo. Entrambi questi fattori possono peggiorare lo stato di conservazione dell'endemico camoscio appenninico.

INTRODUCTION

1.1 Effects of vegetation quality in summer-mid autumn on juvenile mountain ungulates

The availability and quality of food resources influence spatial organisation, foraging behaviour and reproductive success of ungulates (Lovari et al., 1986; Langvatn et al., 1993; Wilmshurst et al., 1995; Gonzales et al., 1996; Anderson et al., 2005; Brambilla et al., 2006; Bocci et al., 2010). In particular, spring and summer are critical periods and the nutritional plane of female ungulates at this time influences the growth and survival of their offspring.

The seasonality of food resources is peculiar of alpine environments. In fact, the snow cover limits the availability of food resources during winter and highly nutritious forage is available only from late spring to early autumn (Moen, 1976; Clutton-Brock et al., 1985; Shackleton and Bunnell, 1987). Because of that, the availability of nutritious summer forage is fundamental for mountain ungulates, which maximise their foraging efficiency and nutrient uptake during summer and mid-autumn, to survive throughout winter (Shackleton and Bunnell, 1987; Bruno and Lovari, 1989; Cook et al., 2004).

In this period, female ungulates have to select nutritious forage, highly digestible and rich in carbohydrates and proteins, to compensate the energy costs of lactation and gestation (Festa-Bianchet et al., 1988, 1997; Pettorelli et al., 2003, 2005, 2007; Ruckstuhl et al., 2003; Ivar Herfindal et al., 2006; Therrien et al., 2008; Hamel et al., 2009; Garel et al., 2011; Ferretti et al., 2015). Then, the use of nutritious forage during summer and mid-autumn influences body conditions of female ungulates during nursing and weaning periods and in turn, the frequency and intensity of maternal

cares (Festa-Bianchet et al., 1988, 1997; Reale et al., 1999; Coté et al., 2001; Hamel et al., 2009).

The amount of maternal cares is expected to affect the growth and survival of ungulate offspring, which is a key determinant for ungulate population dynamics (Clutton-Brock et al., 1984, 1986; Festa-Bianchet et al., 1988, 1997; Pettorelli et al., 2003, 2007; Ivar Herfindal et al., 2006; Marshall et al., 2006; Therrien et al., 2008; Garel et al., 2011). In fact, it has been suggested that, in mountain ungulates, winter survival of offspring strongly depends on body conditions of kids and those of their mothers, during summer period (Clutton-Brock et al., 1984, 1986, 1991; Birgersson and Ekvall, 1997; Festa-Bianchet, 1998). Festa-Bianchet and Jorgenson (1997) suggested that female ungulates adopt a conservative maternal care strategy: during periods of food shortage, females can lose weight, and in turn, they offer less maternal cares to their offspring. In this way, mothers can reduce the risk of their own mortality during winter, thus favouring their lifetime reproductive success but limiting the winter survival of their kids.

If so, a low diet quality of female ungulates during summer, because of an alteration of summer food resources, is expected to affect the winter survival of ungulate offspring and in turn, population dynamics (Gaillard et al., 2000).

Alpine grasslands could be strongly affected by global warming, habitat modifications and the presence of possible competitors which in turn would affect availability and quality of food resources for herbivores (Rossi, 2003; Pettorelli et al., 2007).

It has been suggested that calcareous grasslands of Central Apennine offer nutritious summer pastures for ungulate species (Ferrari et al., 1988; Catorci et al., 2011; Bonanomi et al., 2013). These very diverse-ecosystems are considered priority habitat for the European Union (92/43/EEC Directive).

Alteration in frequency and cover of some alpine plant species could reduce the nutritional quality of summer pastures (e.g. Lovari et al., 2014). Furthermore, the higher temperatures during winter could anticipate the period of green-up of plant species, which might result not synchronized with birth-peak of ungulates (Pettorelli et al., 2005, 2007). The quality of forage depends on its chemical composition (e.g. dry matter, crude protein, fraction of fibers, acid detergent lignin, net energy for lactation) and digestibility (content of fibers, presence of herbivore defense structures with silicon in the leaves in the form of abrasive phytoliths) (Gigon, 1987; Michalet et al., 2002; Catorci et al., 2011; Garbuzov et al., 2011; Kosic et al., 2013). These two parameters vary from June to October and in particular, the digestibility and chemical composition are optimal at the beginning of summer period and they decrease during late summer-early autumn (Ferrari et al., 1988).

Then, the depletion of alpine grasslands and the anticipation of green-up phase caused by global changes, could affect the conservation status of mountain ungulates (Albon and Langvatn, 1992; Langvatn et al., 1996; Inouye et al., 2000; Giacometti et al., 2002; Pettorelli et al., 2005, 2007).

The presence of competitors is another factor that could affect the quality of alpine grasslands (Putman, 1996; Begon, 2006).

Natural ecosystems present an “interactions network” among organisms (Putman, 1996; Latham et al., 1999; Aydt et al., 2008). There are several types of interaction between species belonging to the same trophic level: competition, commensalism, mutualism.

It has been suggested that interspecific competition is the most common interaction between wild ungulates (Latham et al., 1999).

Interspecific competition occurs when two or more species share a scarce resource, with negative effects of the “superior” competitor on growth, fecundity and /or survivorship of the “inferior” one (Begon et al., 2006). Begon et al. (2006) called “superior” competitor the species

generally not affected by the presence of the other one, and “inferior” competitor the species damaged by the former.

Interspecific competition can occur through two mechanisms (Putman, 1996; Latham et al.,1999; Begon et al., 2006): (1) interference, when two species compete through adverse, also physical interactions, as in carnivores (Palomares et al.,1999; Donadio et al., 2006), (2) exploitation of resources, when a species reduces the availability of shared resources for the other ones (Putman, 1996; Latham et al., 1999).

Theoretically, in natural communities coevolved organisms, should coexist without competition, through adaptations which limit competitive interactions, e.g. spatio-temporal partitioning of resources (Putman, 1984; Stephens et al., 1986; Hofmann, 1989; Putman, 1996).

However, several factors could trigger the onset of competition between sympatric species of herbivores (Lovari and Ferretti, 2013): (1) spatio-temporal variation of availability of resources (e.g. seasonality: food shortage during winter, rare and patchily distributed high-quality forage, during spring-summer), (2) habitat modification (e.g. alterations of habitat quality caused by human activities), (3) alteration of natural communities (e.g. translocations of alien species which interact with native ones; elimination of natural predators).

Amongst large ungulates, experimental evidence of competition is lacking (Putman, 1996) even if a few works strongly supported the competition hypothesis (e.g. Forsyth and Hickling, 1998; Hemami et al., 2004, 2005 and references therein; Focardi et al., 2006; Namgail et al., 2009; Richard et al., 2010; Ferretti et al., 2011a-b; Lovari et al., 2014; Ferretti et al., 2015) and in some cases, without explicit considerations on the mechanisms of competition (but see Forsyth and Hickling, 1998; Ferretti et al., 2011b, 2015; Lovari et al., 2014). Most commonly, the degree of habitat and/or diet overlap between species living in sympatry has been considered, without data on population trends which could confirm the decline in numbers of one species and the increase of the other one (e.g. Sinclair et al., 1985; Namgail, 2006; Valeix et al., 2007;

Bertolino et al., 2009). In this way, only a potential of competition can be suspected to occur (Putman, 1996).

Natural communities are complex and controlled experimental conditions could not be representative of natural environments (Putman, 1996). Then, there is a clear difficulty in establishing competition between species in the field. Accordingly, the collection of data applying different techniques could help in evaluating the actual interactions between species, e.g. analyses of overlap in food habits, in relation to food availability, recording of possible behavioural interactions, analysis of population trends, evaluation of habitat/space overlap (Latham et al., 1999).

Competition with a superior competitor can limit the numbers of the inferior competitor, which may affect the conservation status of the latter, if a threatened *taxon* is involved. Thus, understanding the mechanisms that bring to competition can have important implications for the conservation.

Unfortunately, information on the effects of interspecific competition on the intensity of maternal cares, that in turn affect the winter survival of ungulate offspring, have not been documented yet.

1.2 The competition between red deer and Apennine chamois in Abruzzo, Lazio and Molise National Park

The conditions for a competition between red deer *Cervus elaphus* Linnaeus, 1758 and Apennine chamois *Rupicapra pyrenaica ornata* Neumann, 1899 are present in some areas of the Abruzzo, Lazio and Molise National Park (ALMNP, Lovari et al., 2014; Ferretti et al., 2015).

During last centuries, hunting, intense grazing activities of livestock in upper grasslands and wood cutting to extend these patches, modified extensively the landscape (Bonanomi et al., 2013; Lovari and Ferretti, 2013). At the end of XIXth century, the red deer was totally eliminated from this area and the Apennine chamois survived only in the Val di Rose, Camosciara area, its historic core range (Dupré et al., 2001).

From the middle of XXth century, after the foundation of the Abruzzo National Park (1922) a slow recovery of Apennine chamois occured, but again, from 2000-2006, demographic trends turned back negative, with a 40% decline in its core area of distribution (Lovari et al., 2014) because of a great winter mortality of chamois kids (Latini et al., 2011).

In the 1970s, the red deer was re-introduced to the Abruzzo National Park (Apollonio and Lovari, 2001), and today, red deer numbers are still increasing (in 2010: >2500 ind. Latini, 2010). Presently, this deer is present also in areas formerly used only by chamois (Lovari et al., 2014; Ferretti et al., 2015), also at high densities (Latini, 2010: 14 individuals/100ha in the core area of chamois).

A potential for competition between red deer and chamois has been detected through analyses of diet overlap, in the Alps and in the Jesenicky Mts., beside the ALMNP (Schröder and Schröder, 1984; Homolka and Heroldovà, 2001; Bertolino et al., 2009; Lovari et al., 2014: 75-90% of diet overlap).

Forb patches dominated by *Trifolium thalii* and other legumes, (i.e. the best food patches for chamois, Ferrari et al., 1988) are scarce and available only seasonally (between early summer and mid-autumn). In turn, the potential for competition should be great between species sharing the use of these limited food resources. In some areas of the ALMNP, upper grasslands are grazed by both red deer and chamois: in the core area of distribution range of chamois, an almost complete overlap in food habits (>90%) and use of grasslands (>75%) has been reported between these two ungulates (Lovari et al., 2014).

Furthermore in that Area (Val di Rose), a strong decrease of pasture quality has been documented in 2010-2011 with respect to 1980-1982 (when deer were absent from that area), with an increase of unpalatable plant species (*Brachypodium genuense*, *Carduus carlinaefolius*, *Carlina acaulis*) and a decrease of some of the most used ones by chamois (e.g. *Trifolium thalii*, *Plantago atrata, Ranunculus apenninus, Festuca paniculata, Donoricum columnae,* etc) (Lovari et al., 2014).

More recently, the negative effects of use of grasslands by red deer at high densities have been reported on food availability for chamois (through grazing and/or trampling), diet quality and feeding intensity of chamois females (Ferretti et al., 2015).

A further element to analyse is the relationship between resource exploitation by red deer, pasture quality and frequency/intensity of maternal cares of female chamois, and in turn, its effects on winter survival of chamois kids.

In this work, I will evaluate the hypotheses that: (i) the frequency and intensity of maternal cares of chamois females and (ii) survival of chamois kids are lower in areas grazed by deer at high densities than in area not grazed by deer.

1.3 Aspects of biology of the Apennine chamois

The Apennine chamois is a bovid, belonging to the Order Artiodactyla (Perco, 1987; Canalis, 2012; Corlatti et al., 2011, Tab. 1). The systematics of the *Rupicapra* genus underwent a debate, on the last century, (e.g. Lovari and Scala, 1980; Masini and Lovari, 1988; Hammer et al., 1995; Pérez et al., 2002; Crestanello et al., 2009; Rodriguez et al., 2010). According to the currently recognised taxonomy, there are two species belonging to *Rupicapra* genus: *Rupicapra rupicapra* (the Northern chamois, on the European Alps, mountains of central-eastern Europe, Caucasus and mountains of central-eastern Turkey) and *Rupicapra pyrenaica* (the Southern chamois, on the Cantabrics, Pyrenees and central Apennines) (Corlatti et al., 2011; Mustoni et al., 2012). The former presents seven subspecies (*R. r. rupicapra*, Alps, *R. r. asiatica*, Asia minor, *R. r. caucasica*, Caucasus, *R. r. tatrica*, Slovak, *R. r. carpatica*, Carpathian Mountains, *R. r. balcanica*, Balkan Mountains, *R. r. cartusiana,* Chartreuse Alps*)*, the latter includes three subspecies (*R. p. parva,* Cantabrian Mountains, *R. p. pyrenaica,* in the Pyrenees, *R. p. ornata,* central Apennines) (Corlatti et al., 2011).

Tab.1 Systematics of Apennine chamois (Corlatti et al., 2011)

Order	Artiodactyla
Family	Bovidae
Subfamily	Caprinae
Tribe	Rupicaprini
Genus	*Rupicapra*
Species	*Rupicapra pyrenaica*
Subspecies	***Rupicapra pyrenaica ornata***

Most likely, the *Rupicapra* genus originated in Central Asia and, during the lower to middle Pleistocene (*c.* 250000-150000 years ago) a first wave of chamois may have colonized Europe, reaching Central-Southern Apennines and Iberian peninsula (Masini and Lovari, 1988). Later on, a second colonization wave must have occured (80000-60000 years ago), from Asia Minor or North-Eastern Europe to Central and Eastern Europe (Masini and Lovari, 1988; Corlatti et al., 2011).

Out of the three subspecies of *R. pyrenaica*, only the endemic Apennine chamois is listed as Vulnerable by the IUCN (Herrero et al., 2008). Furthermore, it is cited in the Annex II and IV of the UE Habitats and Species Directive, Appendix II of Bern Convention, Appendix II of CITES and it is indicated as "especially protected species" under Italian law n. 157/1992.

The spatial organization of the chamois mostly depends on the availability and quality of food resources, which in turn is limited by the snow cover during winter. In that period, chamois herds live in forest, upper areas of lower altitude and southern exposed. In summer-autumn, mixed herds with females, immatures and kids graze on alpine and sub-alpine meadows (Figure 1), while males use both wood areas and upper grasslands (Lovari and Cosentino, 1986; Bruno and Lovari, 1988; Ferrari et al., 1988; Bruno and Lovari, 1989; Corlatti, 2009; Ferretti et al., 2014).

The Apennine chamois is considered an intermediate feeder (*sensu* Hofmann, 1989): it can use different types of vegetation with different content of fibers, according to the availability: mostly herbaceous species are grazed in summer, in particular those belonging to the Labiatae and Fabaceae families, with a preference for the vegetal community of *Festuco-Trifolietum thalii* (e.g. *Trifolium thalii, Crepis aurea glabrescens, Plantago atrata,* Ferrari et al., 1988), and shrubs, broad-leaved trees and coniferous components in winter. In fact, the leaves of Fabaceae are highly digestible and nutritious because of the presence of more proteins in the two cotyledons than starch in the primary endosperm (the fruits contain more proteins) (Peruzzi L., pers. comm.). Diet quality tends to decrease

throughout summer-autumn: from June to September, there is a decrease in crude protein and an increase of calcium and magnesium and fibers, in plants (Ferrari et al., 1988).

Figure 1. A mixed-herd of Apennine chamois, with females, immatures and kids (Mt. Meta October 2014).

Aims:

In this thesis, I will evaluate:

1) The spatial overlap between the red deer and the Apennine chamois in the use of grasslands, during summer-mid autumn.
2) The effects of (1) on frequency/intensity of suckling behaviour of Apennine chamois.
3) The effects of (1) and (2) on winter survival of chamois kids.

MATERIALS & METHODS

2.1 Study area

Data were recorded from July to October 2013-2014, in three Study Areas located in the Abruzzo, Lazio and Molise National Park (ALMNP), central Apennines, 51 000 ha; Buffer Zone: 80 000 ha (provinces of L'Aquila, Frosinone and Isernia, Figure 2).

ALMNP is a mountainous area and its altitude ranges between 675 m a.s.l. and 2285 m a.s.l. (Mt. Greco). Other important relieves are Mt. Petroso (2249 m a.s.l.), Mt. Marsicano (2245 m a.s.l.) and Mt. Meta (2242 m a.s.l.).

The main river is the Sangro river and the principal lake basin is the artificial Barrea Lake.

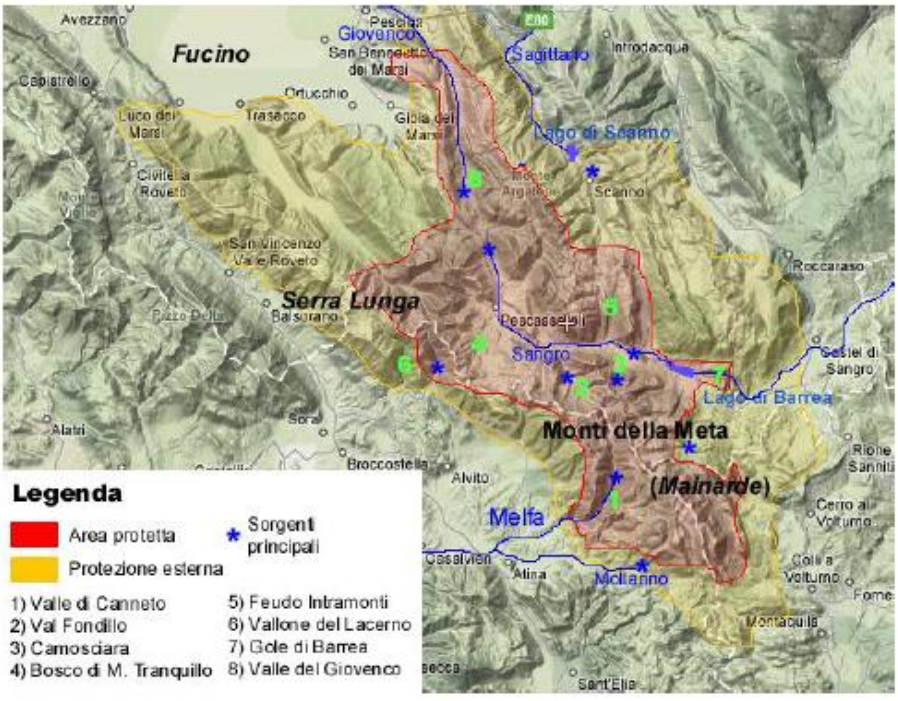


Figure 2. The Abruzzo, Lazio and Molise National Park (in red, the Protected Area; in yellow, the buffer zone; in blue, streams and lakes. from http://www.parcoabruzzo.it/map.php).

Figure 3. The location of my Study Areas (A, B and C) in ALMNP (from Ferretti et al., 2015).

The majority of Park lands are characterized by mixed beech forests (*Fagus sylvatica*) from 1000 m a.s.l. to 1800 m a.s.l.. Upper grasslands are located from *c.* 1800 m a.s.l. to c. 2200 m a.s.l..

The three Study Areas are located in the core protected area of the ALMNP (Figure 3).

They present an alpine and sub-alpine climate, with a snow cover that lasts from November to May-June (Bruno and Lovari, 1989). Yearly rainfall averages 1600-1700 mm in the higher altitudes (Bruno and Lovari, 1989). July and August are hottest months, with daily mean temperatures of 19°C (1986) and 19.4°C (2003) (Troiani, 2011). December, January and February

are the coldest months, with mean daily temperatures of 3°C (1986-2003) (Troiani, 2011).

These three areas are located on alpine grasslands grazed by chamois females and kids, during summer-early autumn, above the tree-line. Area A is in the core area of distribution of the Apennine chamois in ALMNP, (c. 40 ha, Figure 3). The area is delimited by Mt. Sterpalto, Mt. Boccanera and Cavuto Pass (1700–1982 m a.s.l.) (Lovari et al., 2014). Area A presents a strong deplation of summer pastures, respecting to 1982-1984, when red deer was absent from that area (Ferrari et al., 1988; Lovari et al., 2014). This meadows are not grazed by livestock since c. 50 years. Area B (c. 20 ha) is located on upper grasslands of Mt. Amaro (c. 1700-1882 m a.s.l.) (Figure 3). That area is not grazed by livestock since 50. Area C (c. 20 ha, Figure 3) includes the upper meadows of Mt. Meta (c. 2000-2242 m a.s.l.). Peripheral sectors of this are occasionally visited by livestock, in summer-early autumn.

During the study, the three Study Areas were visited by a minimum of 43-53 chamois (Area A), 40-49 chamois (Area B), 79 chamois (Area C) depending on year. These numbers are *c.* 60-70% and 20-30% lower than those in 1975-1980, in area A and B respectively (Mari and Lovari, 2006; Lovari et al., 2014), while mixed herds with females and kids were not present in Area C, in 1975-1980 (Lovari S., pers. comm.). All the Areas lie in the sector of ALMNP with the greatest density of red deer (c. 14 deer/100 ha, in 2010, Latini, 2010). These three areas present palatable graminoids (e.g. *Festuca paniculata*), dicotyledon forbs (e.g. *Ranunculus apenninus*, *Donoricum columnae, Plantago atrata*), including legumes (e.g. *Trifolium* spp. as *Trifolium thalii*) and unpalatable plant species (e.g. *Brachypodium genuense,* a graminoid*, Carduus carlinaefolius* and *Carlina acaulis,* belonging to the Asteraceae family) (Lovari et al., 2014; Ferretti et al., 2015). The roe deer *Capreolus capreolus* and the wild boar *Sus scrofa* visit alpine grasslands occasionally (Lovari et al., 2014) while grey wolf *Canis lupus*, brown bear *Ursus arctos marisucanus* and golden eagle *Aquila chrysaetos* are also present in the ALMNP (Ferretti et al., 2015).

2.2 Methods

Deer/chamois spatial overlap, in grasslands.

The spatial overlap in grasslands between red deer and Apennine chamois has been estimated through the faecal accumulation rate *(FAR)* technique, which is a pellet group count method (Mayle et al., 1999). This technique consists in recording the number of pellet groups of the species of interest, in a certain area, in a given period (Mayle et al., 1999). The pellet group count is an indirect method to evaluate density, spatial distribution, habitat use of ungulate species, in woody or mountainous areas, or for species with nocturnal activity, for which direct counts are unreliable/unfeasible (e.g. Neff, 1968; Mayle et al., 1999).

This technique consists in recording the number of pellet groups (1 pellet group unit must present at least 5 pellets) in sampling areas, in a defined time period: a first survey is conducted to remove all pellet groups from the area and a second survey is conducted after *n* days, to count all pellet groups accumulated in the area, during the sampling time (Mayle et al., 1999). In my case-study, pellet groups were counted in circular sampling plot*s* (radius = 5 m, Fattorini et al., 2011). Plot*s* were visited for a first time at the end of June; then, plots were visited at the end of each month, from July to October, to count/remove all pellet groups of deer and chamois (Lovari et al., 2014; Ferretti et al., 2015), which were identified owing to morphological differences (Mustoni et al., 2002).

Plot*s* were randomly placed onto a grid overlain to grasslands (1 plot/cell; cell size: 100 x 100 m; Area A: *n* = 33, Area B: *n* = 17, Area C: *n* = 21, Figure 4). Centers of plot*s* were marked through a stake to find them during following surveys and I used a GPS device (GarminEtrex) to locate them in the field. I recorded the number of pellet groups found onto check-sheets for the following analyses.

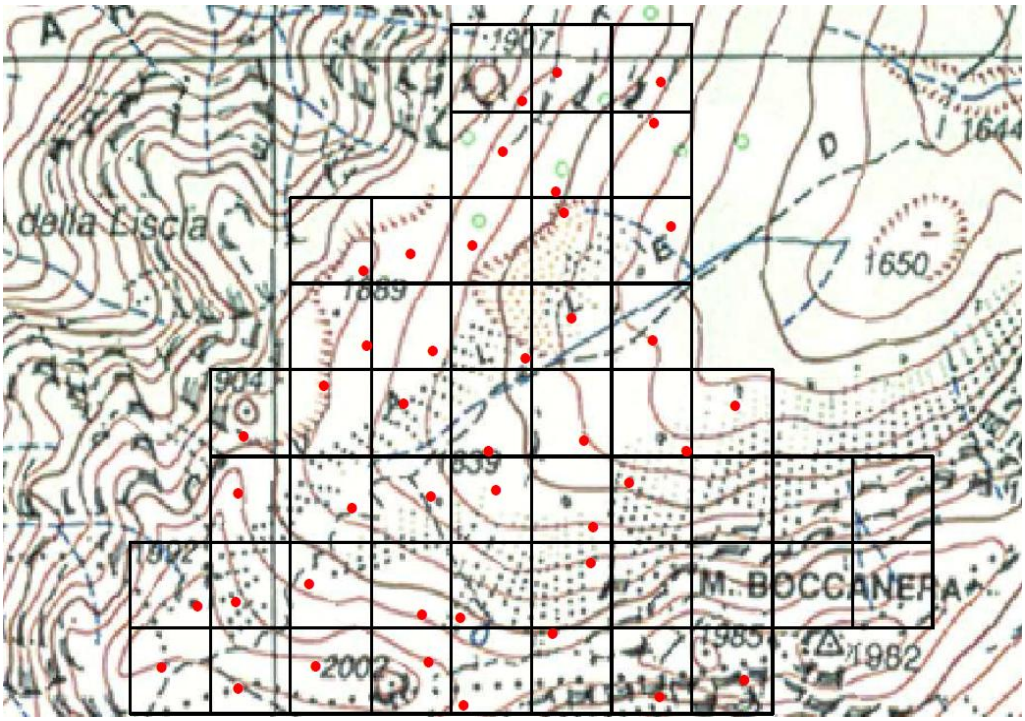


Figure 4. Sampling plots, in red, in Area A.

We used circular plots to minimize the "edge effect" (i.e. the problem of counting pellet groups found at the limit of the plot area), because the circular shape raises the minimum ratio of perimeter/surface rather than a square form (Fattorini et al., 2011). Furthermore, this plot-grid dispersion determines a more homogeneous plot distribution in the areas, than the one which could be produce by a purely random design and it is particularly suitable for group-living animals like red deer and chamois. In fact, the possibility of covering the whole areas prevents the risk of analysing only patches used or not used by the species of interest.

Frequency and intensity of chamois maternal cares and winter survival of chamois offspring: behavioural observations

Generally, researchers conduct behavioral observations to estimate the amount of maternal cares (Festa-Bianchet et al., 1988, 1997; Hass, 1990; Lavigueur, 1992; Clark and Odell, 1999; Cassinello, 2001; Therrien et al., 2008; Pluhácek et al., 2013).

In particular, the focal animal sampling method is usually used to evaluate the frequency, duration and temporal sequences of certain behaviours, observing continually one or more individuals, for a certain time interval (Lovari and Rolando, 2004: 95). This method is useful to record rare and occasional events as a suckling events. On the contrary, the scan sampling is a discontinuous sampling (Mitlöhner et al., 2001), generally used to evaluate state behaviours (behaviours exhibited for a period of time as sleeping, walking, foraging etc): a group or an animal is scanned instantaneously at set time interval, recording whatever the group or the animal is doing in that moment.

In my case-study, I conducted behavioural observations on kid-female groups to evaluate the frequency and intensity of maternal cares of chamois females, as well as to estimate the winter survival of chamois kids, during the period of nursing and weaning. Data were recorded during 6-8h of bouts/day, covering homogenously different times of the day across the study areas in 6-8 sampling days/area/month, using a Nikon 20-60X telescope and Nikon 16X50 binoculars, with a distance of 30-200m from the chamois groups (Bruno and Lovari, 1988).

The observations were divided in 30min sampling intervals applying the focal animal sampling technique, wherewith we recorded in specific sheets (Figure 5): (1) N. and duration of suckling events (the duration was recorded with a chronometer) (Festa-Bianchet, 1988), (2) N. of unsuccessful attempts (Festa-Bianchet, 1988), and (3) N. of aggressions of adults to kids.

Area: VR **Date:** 14/07/14 **Observer:** SB

Interval	h	Type*	Duration	Stop**	Activity F***
1	5:42	S	43	F	G
1	5:46	R			
1	5:59	S	56	I	G
1	5:59	S	18	I	G
1	5:59	S	7	I	G
2	6:18	L			
2	6:26	S	19	F	L
...					

Figure 5. An example of form for the focal animal recording (*type: S = suck, R = rejection, L = licking; **stop, who stops the suckling event: F = female, K = kid, I = indeterminate; ***activity F, what the female was doing before the suckling event: G = grazing, L = laying, O = other).

I considered as suckling attempts all the cases in which the kid approached the mother breasts. Attempts were considered successful when the kid started suckling and the bout lasted at least 5s (Festa-Bianchet, 1988). Attempts were considered unsuccessful when the female moved away interrupting the suck event after less than 5s or when the female did not allow the kid to start suckling (Festa-Bianchet, 1988; Engelhardt et al., 2014). I used the suckling duration and the frequency of suck bout as parameters for the suckling intensity (Festa-Bianchet, 1988).

I recorded the number of kids, group size and structure every 5min, through the scan sampling method. I considered a group when there were at least two individuals, at a mutual distance lower than 40m (Bruno and Lovari, 1989). Furthermore, to estimate group structure, sex/age classes were estimated observing the ear-horn length, the horn size and the presence of the penile tuft (Lovari, 1985).

I considered the following age classes (Lovari, 1985; Figure 6):

(1) kids: the new born individuals, completely dependent on their mothers;

(2) yearlings: individuals of one year. The horn length is around the ears one;

(3) subadults (2-3 years old): the horns are *c.* ¼ - ⅓ longer than the ears;

(4) young adults (4-5 years old): individuals developed for a reproductive and morphological point of view. The horns are *c*. ½ longer than the ears;

(5) mature adults (6-8 years old): individuals completely developed for a reproductive and morphological point of view. The horns are *c*. twice the ears;

(6) fully mature adults (>8 years old): The horns are twice over the ears.

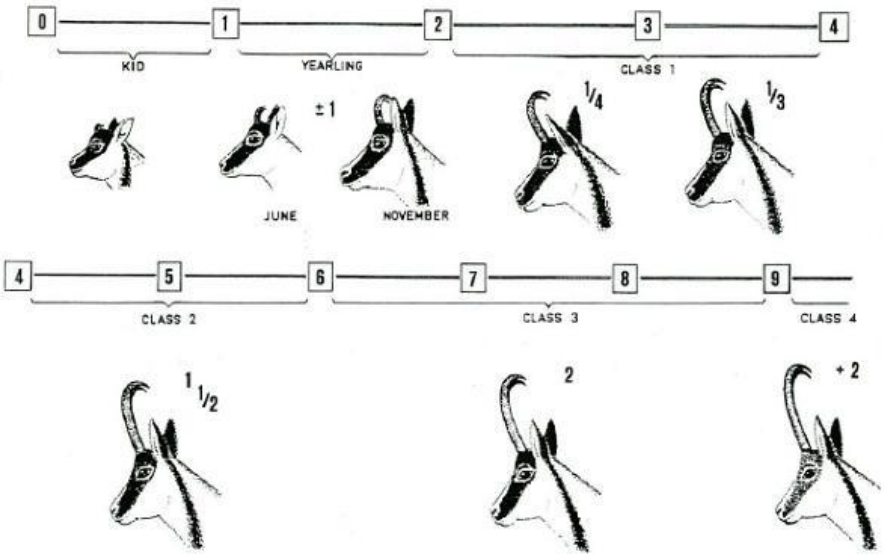


Figure 6. Age classes of the Apennine chamois (from Lovari, 1985).

2.3 Analyses

For the analyses, I used data recorded July-October, 2013-2014.

Spatial overlap of red deer/chamois and pellet group density of red deer

Data recorded through the fecal accumulation rate technique (N. of red deer/chamois pellet groups and red deer/chamois presence) were collected in computer datasets (Microsoft Office © Excel) for the following analyses, which were conducted through the R (2.15.0, R Development Core Team 2012) and Microsoft Excel (Microsoft Office © Excel) software.

I evaluated the spatial overlap of red deer/chamois in all the plots (I_{tot}) and only in plots used by chamois (I_{cam}), through the Jaccard index (Jaccard, 1901):

$I_{tot} = A / (A + B + C)$

$I_{cam} = A / (A + B)$

where:

A = N. of plot with pellet groups of both species, in July-October
B = N. of plot with chamois pellet groups, only in July-October
C = N. of plot with red deer pellet groups, only in July-October

Furthermore, I evaluated the pellet group density of red deer in the three areas, corresponding to the mean N. of red deer pellet groups/plot in July-October. The pellet group density is generally used to evaluate indirectly the density of a species (Mayle et al., 1999).

Then, I compared the spatial overlap and red deer relative density across the three areas through generalised linear mixed models (GLMMs, Kachman, 2000; Crawley, 2007). I used a GLMM with binomial error for the spatial overlap, considering the red deer presence in plots in July-October

as the response variable; predictors were Area and Year. Plot identities were fitted as random effects.

The difference of red deer density across the three areas was evaluated through a GLMM (Kachman, 2000; Crawley, 2007), with Poisson error, considering the N. of red deer pellet groups in plots in July-October ($N_{red\ deer}$) as the response variable and the predictors were the Area and the Year. Plot identities were fitted as random effects.

For both analyses, I estimated minimum adequate models by removing the least significant predictor at each step, until the elimination of predictors determined a significant increase in the residual deviance, which was evaluated through Chi-square tests (Crawley, 2007).

Intensity of chamois maternal cares

The intensity of chamois maternal cares was evaluated using data recorded during the behavioral observations. Data were collected in computer datasets (Microsoft Office © Excel) for the following analyses, which were conducted through the R (2.15.0, R Development Core Team 2012) and Microsoft Excel (Microsoft Office © Excel) software.

In all the three study-areas, I evaluated the following indices of maternal cares:

- probability of suckling success (N. successful suckling events / N. of suckling attempts)
- suckling rate (N. successful suck bouts in the *i* interval / N. of kids in the *i* interval / duration of the *i* interval)
- suckling attempt rate (N. suckling attempts in the *i* interval / N. of kids in the *i* interval / duration of the *i* interval)
- suckling duration (in seconds)
- suckling intensity (the product between the suckling duration and the suckling rate)

I also evaluated the aggression rate of the adults to the kids, during the grazing activity (N. aggressions in the *i* interval / N. of kids in the *i* interval / duration of the *i* interval). All the frequencies were standardized on hourly basis (N. events / kid / h).

After, I compared the different indices across the three areas through generalised linear mixed models (GLMMs), with binomial errors (for the probability of suck bouts) and Poisson errors (for frequencies and durations).

For the probability of suckling success I used a GLMM (Kachman, 2000; Crawley, 2007) with binomial error, in which the successful (1) / unsuccessful (0) attempt was the response variable. Area, Season (summer: July-August, autumn: September-October), Year and AreaxSeason-interaction were the predictors. The hour (divided by 1 h time intervals) and the date were fitted

as random effects to control for repeated observations in the same days or in the same hour. Minimum adequate models were estimated through the procedure described above.

For the comparison of suckling rate, suckling attempt rate and aggression rate, as well as suck duration, I used GLMMs (Kachman, 2000; Crawley, 2007) with Poisson errors. Rates (in classes: 0 events/kids/hour = 0; 0.01-0.1 = 1; 0.11-0.2 = 2; 0.21-0.3 = 3; etc.), or duration were response variables. Area, Season, Year and AreaxSeason-interaction were the predictors. Hour and date were fitted as random effects. Minimum adequate models were estimated through the procedure described above.

Winter survival of chamois offspring

In the three areas I evaluated:

- index of winter survival of chamois offspring (N. *yearlings* of the current year in July / N. kids counted in the previous year
- birth rate (N. chamois kids / N. adult females)

For the N. of kids, yearlings and adult females I considered the maximum N. of them counted at the same time (Lovari et al., 2014; Ferretti et al., 2015).

After, I compared the winter survival across the three areas, using a GLM (Kachman, 2000; Crawley, 2007) with binomial error. The response variable was coded as follows: for each study-area, in each year, if K_0 = N. of kids counted in the year 0 and Y_1 = N. of yearlings counted the following year 0 + 1, then we assigned Y_1 "1" values (i.e. kid survived) and K_0 - Y_1 "0" values (i.e. kid dead). The Area and the Year were the *predictors*. The minimum adequate models were estimated through the procedure described above. The birth ratio was compared across Areas through the G-test.

RESULTS

I recorded data through 34 field surveys (July-October 2014, total hours: 234). Besides, I analysed data collected in July-October 2013-2014 by other observers. Throughout the study period, 700 pellet group count surveys were conducted and 1292 sampling intervals for analyses of maternal cares were carried out during 646h of observations. I have recorded 204 sampling intervals of 30 min (total hours of observation: 102). Overall, 1960 suckling attempts were recorded: 842 out of these were successful (43%). In particular, 616 suckling attempts were recorded in Area A (N. successful attempts: 236, 38%), 426 in Area B (N. successful attempts: 159, 37%) and 918 in Area C (N. successful attempts: 447, 49%).

Deer/chamois overlap and density of red deer pellet groups

The spatial overlap in grasslands used by chamois was almost complete in Areas A and B (I_{cam}: Area A: 0.93, Area B: 0.84) and very low in Area C ($I_{cam,}$ Area C: 0.10) (Figure 7, Tab. 2).

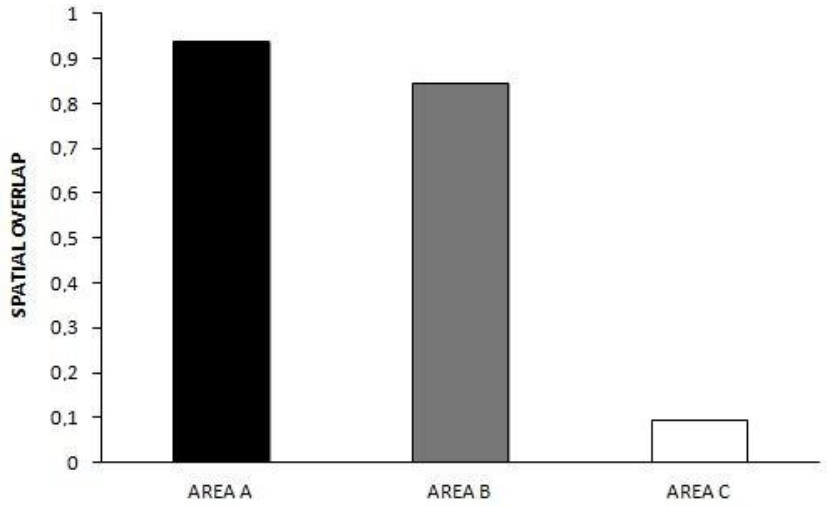


Figure 7. Deer/chamois spatial overlap in the use of grasslands: proportion of plots used by chamois with red deer pellet groups in July-October 2013-2014 in three study-areas, estimated through pellet group counts in circular sampling plots (Area A, *n* = 33; Area B, *n* = 17; Area C, *n* = 21).

Tab. 2. Deer/chamois overlap in grasslands: N. plots (Area A, *n* = 33/year, Area B, *n* = 17/year, Area C, *n* = 21/year) with pellet groups of chamois, red deer and both species (July-October, 2013-2014); I_{tot} = spatial overlap index in the total area, I_{cam} = spatial overlap index in plots used by chamois.

Study Area	Only chamois	Only red deer	Both species	I_{tot}	I_{cam}
Area A	3	18	45	0.68	0.94
Area B	5	2	27	0.79	0.84
Area C	38	0	4	0.10	0.10

In particular, the spatial overlap between deer and chamois was significantly greater in Area A and Area B, than in Area C and it did not differ significantly between Areas A and B (Tab 3).

Tab. 3. Differences across Areas in spatial overlap in grasslands between red deer and Apennine chamois, in July-October 2013-2014, estimated through pellet group counts in circular sampling plots (Area A, *n* = 33/year, Area B, *n* = 17/year, Area C, *n* = 21/year) and GLMMs with binomial errors; the minimum adequate model is shown.

Predictors	*B*	*S.E.*	*P*
Intercept	8.218	2.070	< 0.001
Area[B]	-1.172	2.105	0.578
Area[C]	-15.585	3.549	< 0.001

The density of red deer pellet groups (N. pellet groups / plot in July-October) was the greatest in Area A, intermediate in Area B and negligible in Area C (Figure 8).

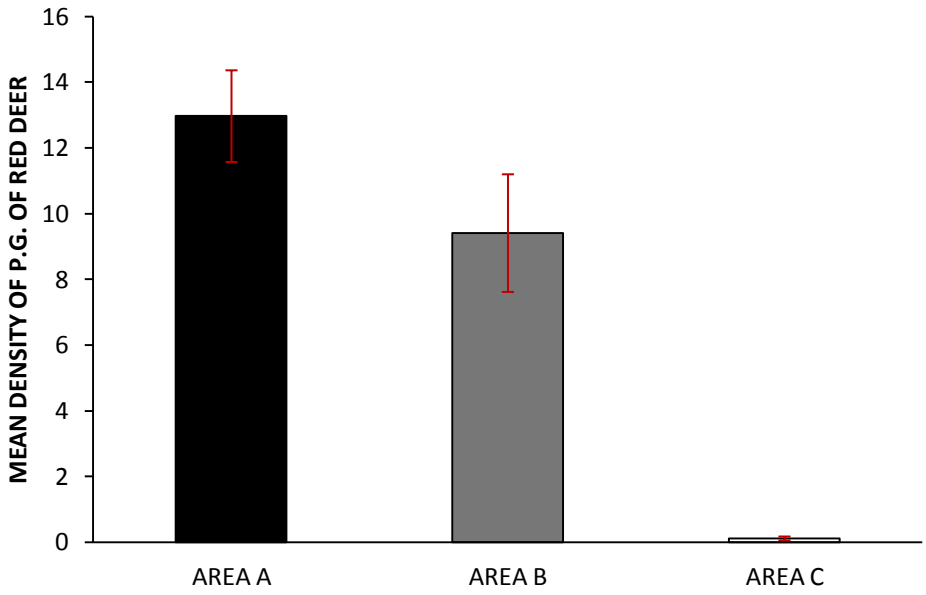


Figure 8. Density of pellet groups of red deer in July-October (2013-2014, mean ± standard error) estimated through pellet group counts in circular sampling plots (Area A, *n* = 33/year; Area B, *n* = 17/year; Area C, *n* = 21/year).

The density of red deer pellet groups, i.e. the index of red deer density, was significantly the lowest in Area C, while it did not differ significantly between Area A and Area B (Tab. 4).

Tab 4. Differences across Areas in pellet group density of red deer, in July-October 2013-2014, estimated through pellet group counts in circular sampling plots (Area A, n = 33/year, Area B, n = 17/year, Area C, n = 21/year) and GLMMs with Poisson errors; the minimum adequate model is shown.

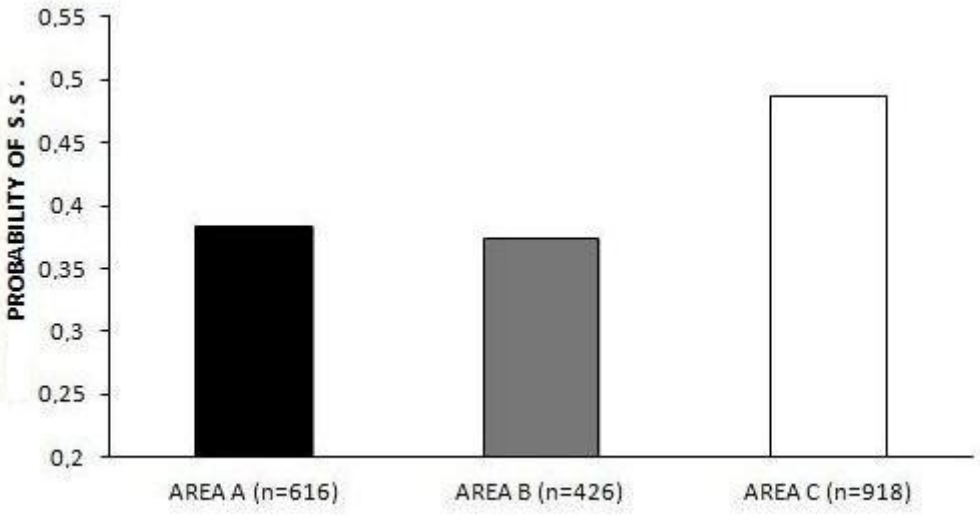
Predictors	*B*	*S.E.*	*P*
Intercept	2.148	0.191	< 0.001
Area[B]	-0.413	0.330	0.210
Area[C]	-4.784	0.565	< 0.001

These results suggested a very high spatial overlap between red deer and chamois in grasslands of Areas A and B, while Area C was regularly grazed only by chamois.

Chamois maternal cares

Almost all the suck bouts were interrupted by females (Area A: 100%, Area B e Area C: 98%). The probability of suckling success was significantly the greatest in Area C (Area A: 0.38, Area B: 0.37, Area C: 0.49, Figure 9, Tab. 5). Thus, in Area C the probability of suck success was greater by 27% and 31% than in Areas A and B, respectively. At the bimonthly temporal scale, the probability of suck success was constantly greater in Area C than in Area A and Area B (summer: Area A = 0.40; Area B = 0.38; Area C = 0.49; autumn: Area A = 0.32; Area B = 0.36; Area C = 0.48, Figure 9). Although, the bimonthly probability of suck success appeared to decreased from summer to autumn in Area A and – slightly - in Area B, it did not differ significantly between periods.

a)



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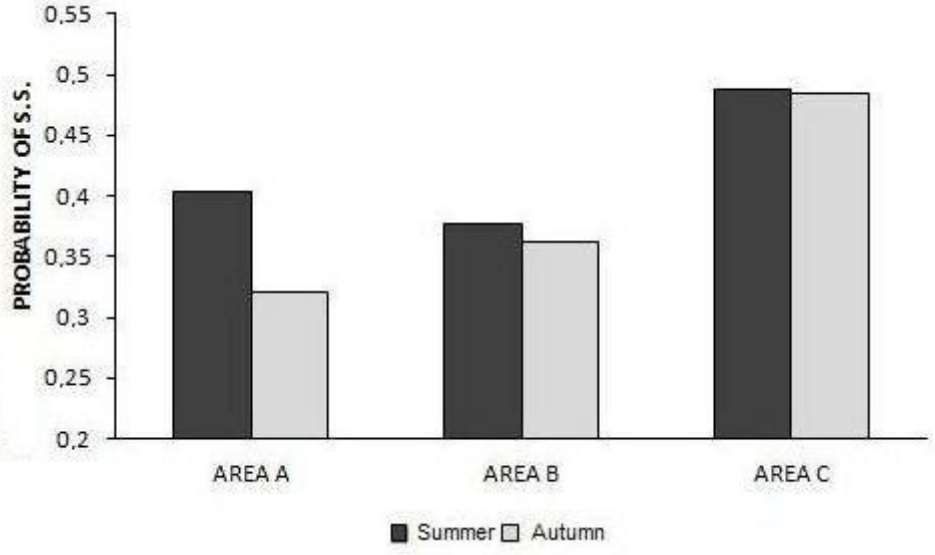


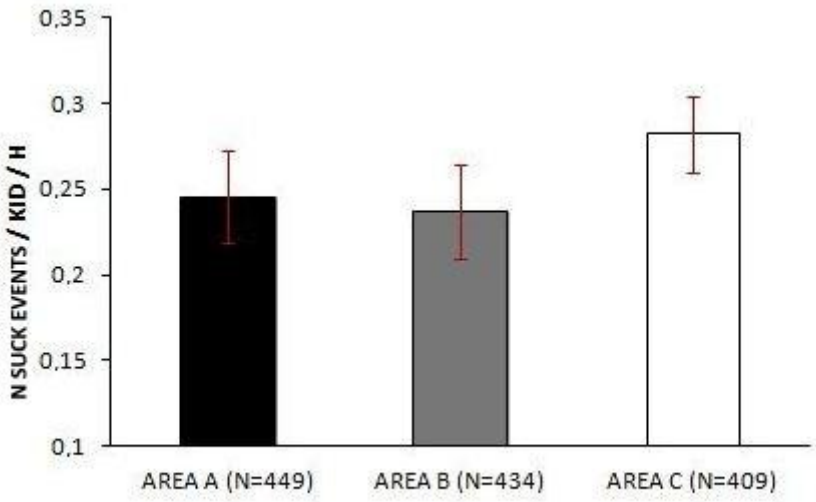
Figure 9. Probability of suckling success of Apennine chamois kids (S.S.: N. suck success / N. suck attempts) at total (a) and bimonthly (b) temporal scales, in three Areas with different densities of red deer pellet groups (Area A: high density, Area B: intermediate density, Area C: red deer absent), in July-October (2013-2014). (a): sample sizes (N attempts) are under the *x* axis. (b): *n* = 466 attempts in Area A (summer), *n* = 150 (autumn); Area B: *n* = 335 (summer), *n* = 91 (autumn); Area C, *n* = 633 (summer), *n* = 285 (autumn).

Tab. 5. Variables influencing the probability of suck success by Apennine chamois kids in three Areas with different densities of red deer pellet groups (Area A: high density, Area B: intermediate density, Area C: red deer absent), in July-October (2013-2014) estimated through GLMMs with binomial errors (failure: 0; success: 1; N. attempts: 616 in Area A, 426 in Area B, 918 in Area C); the minimum adequate model is shown.

Predictors	*B*	*S.E.*	*P*
Intercept	-0.479	0.107	< 0.001
Area[B]	-0.022	0.153	0.886
Area[C]	0.425	0.132	< 0.001

The suckling rate was higher in Areas C (mean ± standard error: 0.28 ± 0.02 suck events / kid / h) than in Areas A and B (Area A: 0.25 ± 0.03, Area B: 0.24 ± 0.03, Figure 10). Thus, in Area C, the suckling rate was greater by 15% and 19% than in Areas A and B, respectively. The suckling rate was significantly influenced by Area and Season (Tab. 6). In particular, the suckling rate was significantly higher in Area C than in Areas A and B and it decreased significantly from summer to autumn, in all the Areas (Figure 10, Tab. 6).

(a)



(b)

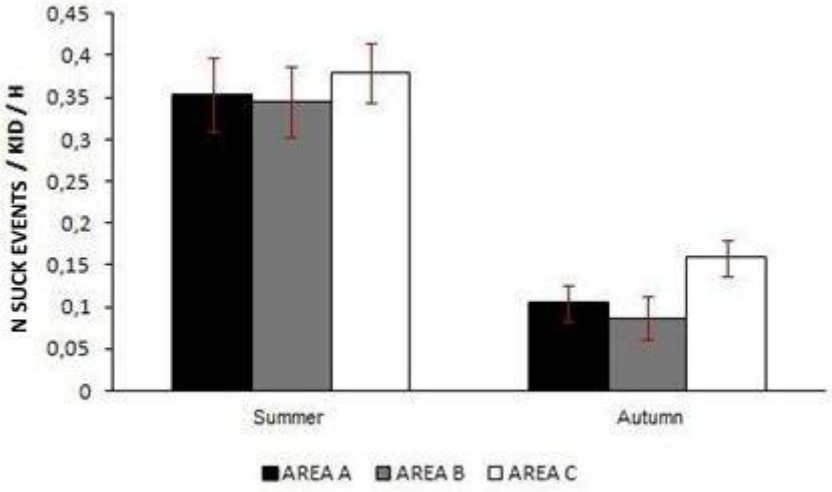


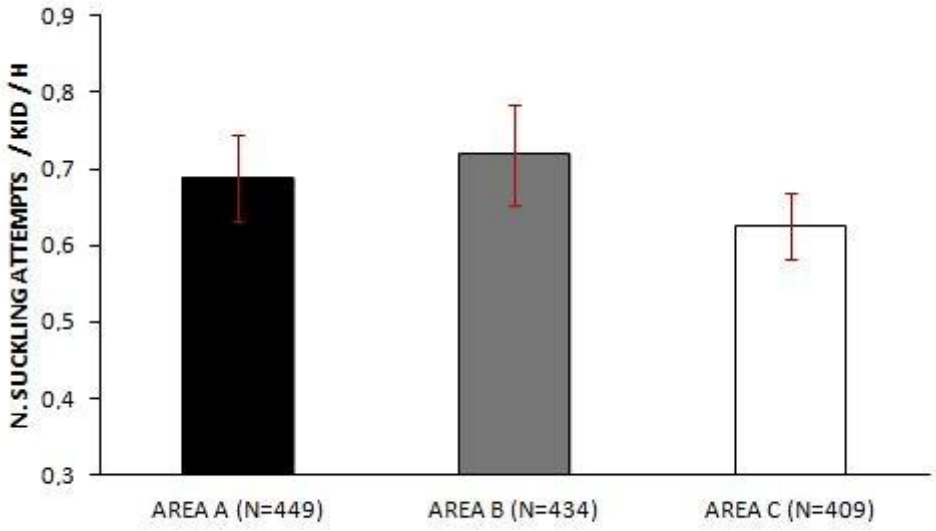
Figure 10. Total (a) and bimonthly (b) frequency of suckling (2013-2014: July-October, mean ± standard error) in the three areas, differing in red deer density (Area A: high density; Area B: intermediate density; Area C: red deer absent). In (a), sample sizes (N. sampling intervals) are under the *x* axis. In (b), Area A: *n* = 253 (summer), *n* = 196 (autumn); Area B: *n* = 252 (summer), *n* = 182 (autumn); Area C, *n* = 228 (summer), *n* = 181 (autumn).

Tab. 6. Variables influencing the suckling rate by Apennine chamois kids in three Areas with different densities of red deer pellet groups (Area A: high density, Area B: intermediate density; Area C: red deer absent), in July-October (2013-2014) estimated through GLMMs with Poisson errors. The minimum adequate model is shown.

Predictors	*B*	*S.E.*	*P*
Intercept	1.149	0.129	< 0.001
Area[B]	-0.110	0.091	0.227
Area[C]	0.209	0.086	0.016
Season[autumn]	-1.309	0.140	< 0.001

The suckling attempt rate was higher in Areas A and B than in Area C (Area A: 0.69 ± 0.06 suckling attempts / kid / h, Area B: 0.72 ± 0.07, Area C: 0.63 ± 0.04, Figure 11). Thus in Area C, this index was lower by the 9% and 13% than in Areas A and B, respectively. The GLMM showed significant effects of Area, Season and interaction Area x Season on the suck attempt rate. The frequency of suckling attempt was significantly lower in Area C during summer and it decreased significantly in autumn, in respect to period, in all the Areas (Tab. 7, Figure 11).

(a)



(b)

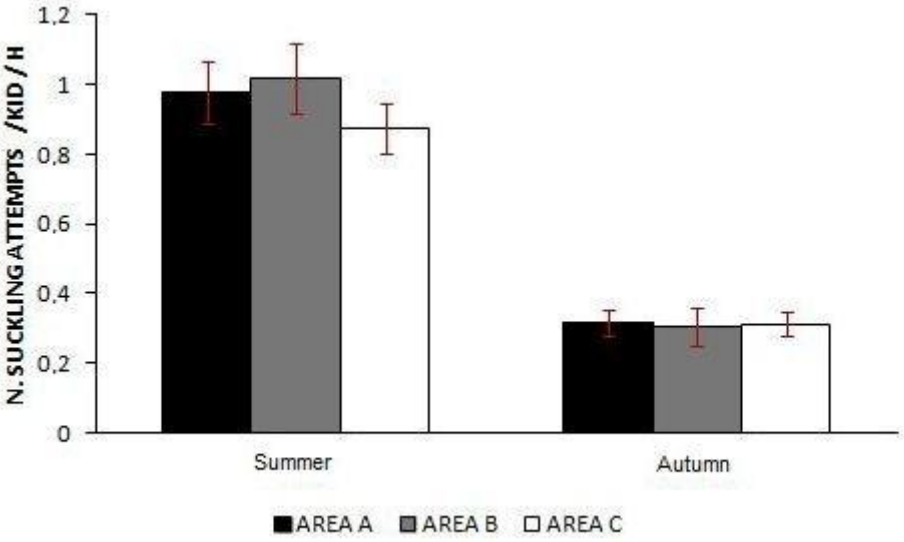


Figure 11. Total (a) and bimonthly (b) frequency of suckling attempt (2013-2014: July-October, mean ± standard error) in the three areas, differing in red deer density (Area A: high density; Area B: intermediate density; Area C: red deer absent). In (a), sample sizes (N. sampling intervals) are under the *x* axis. In (b), Area A: *n* = 253 (summer), *n* = 196 (autumn); Area B: *n* = 252 (summer), *n* = 182 (autumn); Area C, *n* = 228 (summer), *n* = 181 (autumn).

Tab. 7. Variables influencing the suckling attempt rate by Apennine chamois kids in three Areas with different densities of red deer pellet groups (Area A: high density; Area B: intermediate density; Area C: red deer absent), in July-October (2013-2014) estimated through GLMMs with Poisson errors. The minimum adequate model is shown.

Predictors	*B*	*S.E.*	*P*
Intercept	1.853	0.130	< 0.001
Area[B]	0.117	0.068	0.086
Area[C]	0.037	0.063	0.550
Season[Autumn]	-0.803	0.152	< 0.001
Year[2014]	0.317	0.124	< 0.010
Area[B] × Season[Autumn]	-0.926	0.136	< 0.001
Area[C] × Season[Autumn]	-0.383	0.167	0.021

The aggression rate tended to be greater in Areas A and B than in Area C (Area A= 0.12 ± 0.03 suffered aggressions / kid / h; Area B = 0.10 ± 0.03; Area C = 0.08 ± 0.02, Figure 12). Thus, in Area C this index appeared to be lower 32% and 21% than in Areas A and B, respectively. However, differences were not significant across the Areas (GLMM: P > 0.05), probably because of the low quantity of recorded aggressions (N_{total} = 129; Area A, *n* = 37; Area B, *n* = 28; Area C, *n* = 64).

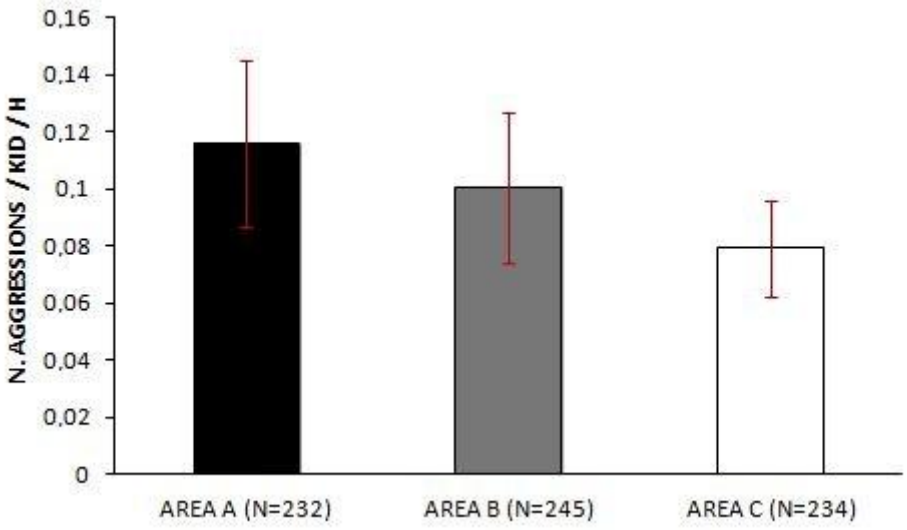


Figure 12. Frequency of aggressions (2013-2014: July-October, mean ± standard error) in the three areas, differing in red deer density (area A: high density; area B: intermediate density; area C: red deer absent). Sample sizes (N. sampling intervals) are under the *x* axis.

The suckling duration was significantly the highest in Area C and the lowest in Area A (Tab. 8): this index decreased significantly from summer to autumn in all the Areas (Summer: Area A = 22.1 ± 0.9 sec; Area B = 26.7 ± 1.2 sec; Area C = 26.6 ± 0.9 sec; Autumn: Area A = 18.8 ± 1.2 sec; Area B = 20 ± 1.7 sec; Area C = 19.6 ± 0.9 sec, Figure 13).

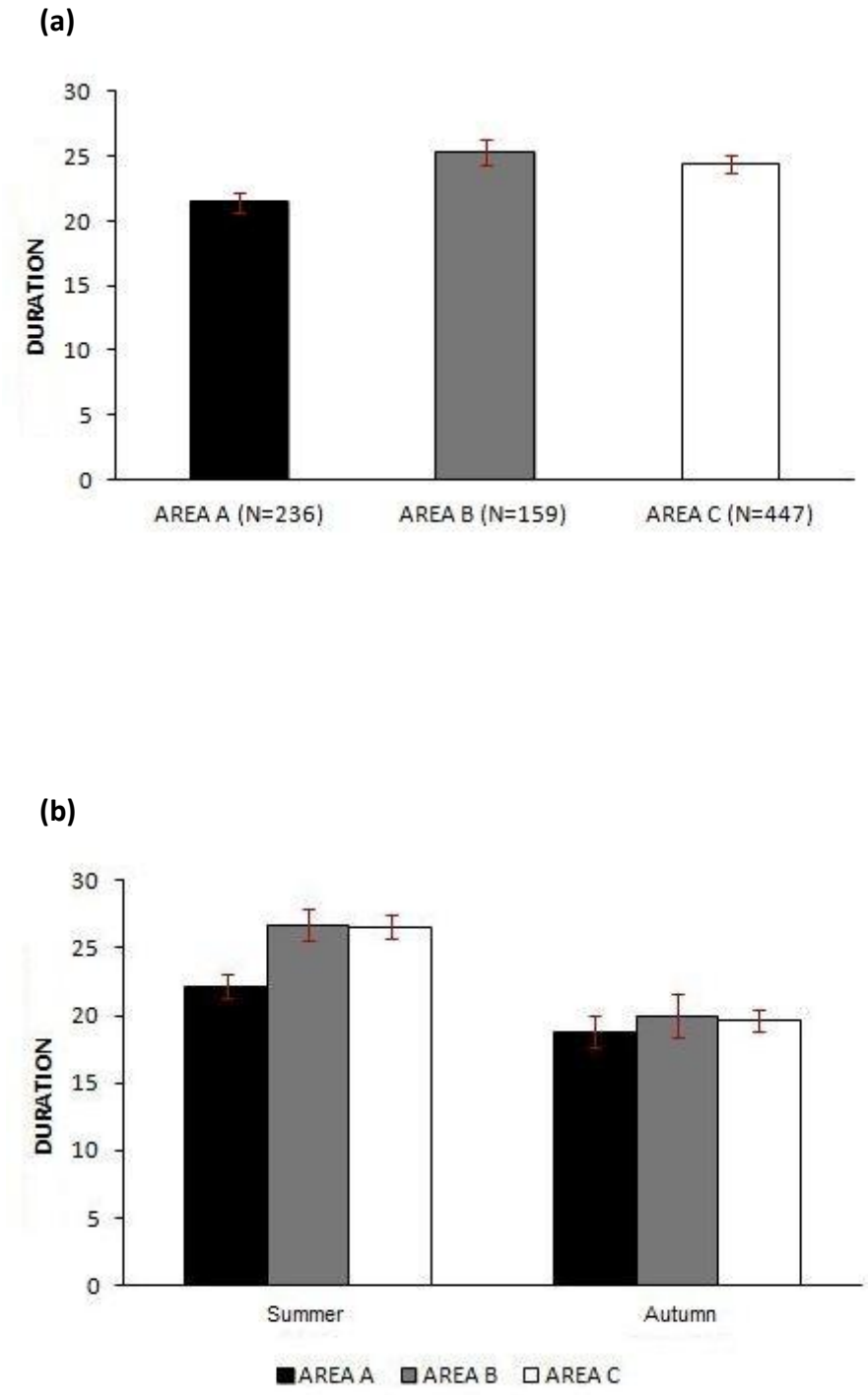


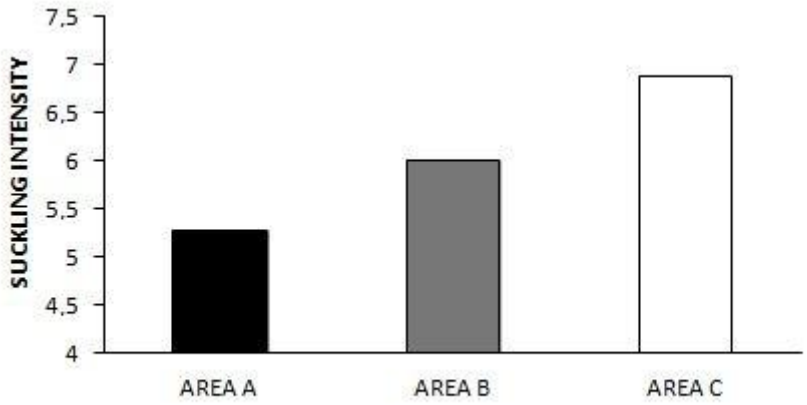
Figure 13. Total (a) and bimonthly (b) suckling duration in seconds (2013-2014: July-October, mean ± standard error) in the three areas, differing in red deer density (Area A: high density; Area B: intermediate density; Area C: red deer absent). In (a), sample sizes (N. suckling events) are under the *x* axis. In (b), Area A: *n* = 188 (summer), *n* = 48 (autumn), Area B: *n* = 126 (summer), *n* = 33 (autumn), Area C, *n* = 309 (summer), *n* = 138 (autumn).

Tab. 8. Variables influencing the suckling duration by Apennine chamois kids in three Areas with different densities of red deer pellet groups (Area A: high density; Area B: intermediate density; Area C: red deer absent), in July-October (2013-2014) estimated through GLMMs with Poisson errors. The minimum adequate model is shown.

Predictors	*B*	*S.E.*	*P*
Intercept	3.343	0.063	< 0.001
Year[2014]	-0.276	0.065	< 0.001
Area[A]	-0.199	0.063	< 0.001
Area[C]	0.119	0.057	< 0.046
Season[Autumn]	-0.231	0.067	< 0.001

Combining the mean suckling duration and the mean suckling rate, I obtained an index of suckling intensity (Area A = 5.4; Area B = 6.1; Area C = 6.8 Figure 14). In Area C, this index was greater by 31% and 15% than in Areas A and B, respectively. These results were confirmed also at the bimonthly scale, with the greatest values in Area C, intermediate ones in Area B and the lowest ones in Area A, as well as decrease from summer to autumn (Summer: Area A = 7.8, Area B = 9.2, Area C = 10.1; Autumn: Area A = 2.0, Area B = 1.7, Area C = 3.1, Figure 14).

(a)



(b)

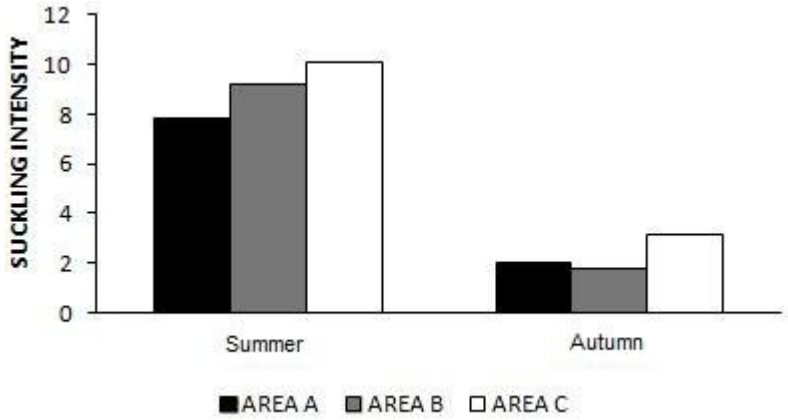


Figure 14. Total (a) and bimonthly (b) suckling intensity (2013-2014: July-October, i.e. mean suck frequency x mean suck duration) in the three areas, differing in red deer density (Area A: high density; Area B: intermediate density; Area C: red deer absent).

Winter survival of chamois offspring

The index of winter survival of chamois kids was significantly the greatest in Area C (Area A = 0.19, Area B = 0.25, Area C = 0.45, Figure 15, Tab. 9). The birth ratio did not differ significantly across Areas and it ranged from 0.56 kids / adult female to 0.63 kids / adult female (G-test: $P > 0.05$).

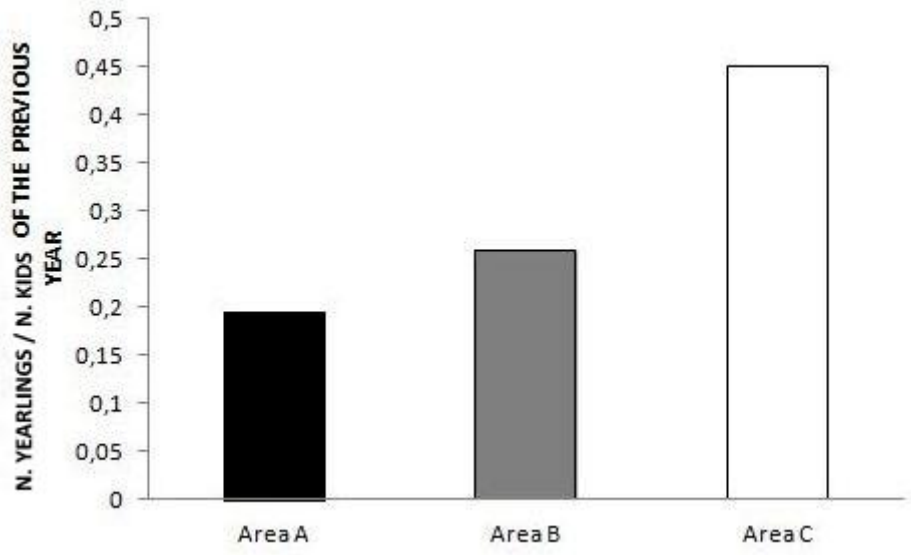


Figure 15. The winter survival of chamois offspring (2013-2014: July-October) in the three areas, differing in red deer density (Area A: high density; Area B: intermediate density; Area C: red deer absent).

Figure 9. Variables influencing the winter survival of Apennine chamois kids in three Areas with different densities of red deer pellet groups (Area A: high density, Area B: intermediate density, Area C: red deer absent), in July-October (2013-2014) estimated through GLMMs with binomial errors. The minimum adequate model is shown.

Predictors	*B*	*S.E.*	*P*
Intercept	-1.953	0.520	< 0.001
Year[2014]	1.019	0.492	< 0.038
Area[B]	0.274	0.622	0.659
Area[C]	1.496	0.566	< 0.008

DISCUSSION

My results suggested that suckling behaviour of Apennine chamois was more intense (greater suckling success; higher frequencies of suck events and suck duration; comparatively lower rates of suck rejections) in the Area with the greatest pasture quality and which was not grazed by red deer than in the two Areas intensively used by deer also (Lovari et al., 2014; Ferretti et al., 2015). Furthermore, winter survival of chamois kids was greater in the former than in the latter. These results supported the hypothesis that a reduction of availability and quality of key-food resources, in summer-early autumn, affects diet quality and foraging efficiency of adult female chamois, in turn reducing intensity and frequency of maternal cares, ultimately limiting winter survival of offspring (Lovari et al., 2014; Ferretti et al., 2015).

Environmental conditions, such as depth and persistence of snow cover, as well as temperature, are regarded as important factors influencing spatial behaviour and foraging efficiency of many ungulate species (e.g. Clutton-Brock et al. 1985; Grignolio et al., 2004; Pettorelli et al., 2005). In particular, low temperatures and snow cover limit the availability of food resources during winter, while nutritious pastures are present only during summer (Ferrari et al., 1988). Mountain ungulates are limited by environmental alterations that affect the availability and quality of nutritious summer pastures (Festa-Bianchet et al., 1998; Pettorelli et al., 2007; Therrien et al., 2007). In turn, these ungulates have to focus their energy uptake between late spring and early autumn, optimizing their foraging efficiency to store the fat reserves necessary for winter survival (Shackleton & Bunnell 1987; Pettorelli et al. 2007; Rughetti & Festa-Bianchet 2012). Furthermore, the birth peak usually occurs in a period wich allows females and offspring to use high-quality, fresh vegetation during nursing/weaning periods, when females have to compensate the high energy costs of lactation and gestation manly during summer (Clutton-Brock et al. 1989). The nursing period makes female lose energies and body

reserves, with the risk of affecting their subsequent reproduction and survival (Clutton-Brock et al., 1989; Rogowitz, 1996; Carlini et al., 2004). Then, during a period of food shortage, mothers adopt a trade-off between caring for their offspring and their physical maintenance, which would enhance their survival and future reproductive success (Holand et al., 2006; Therrien et al., 2007). In particular, in the case of food depletion and low kid survival, iteroparous females will decrease the intensity of maternal cares, favoring their own survival and their subsequent reproduction, according to a conservative reproductive strategy (Berger, 1979; Clutton-Brock, 1991; Therrien et al., 2007). A reduction of frequency of maternal cares alters the growth and body mass of offspring and then, depletion of food resources mainly affects survival of juveniles more than that of adults (Fowler, 1987; Moorcroft et al., 1996; Owen-Smith, 1990). Thus, a decrease of availability and quality of summer pastures could emphasize the mother-kid conflict (Trivers, 1974; Berger, 1979) and, in turn, could affect the winter survival of ungulate offspring (Festa-Bianchet and Jorgenson, 1997; Therrien, 2008).

My results showed that probability of suckling success was significantly greater in Area C than in Areas A and B. This index indicates the tendency of the mothers to allow kids to suck (Berger, 1979). In case of limitation of food resources, the availability of milk is lower and mother rejections are more frequent (Berger, 1979, Therrien et al., 2007). On the contrary, females will be more willing to allow lactation in the case of higher availability of milk (Berger, 1979). In Area C, the availability and quality of summer pastures are greater, suggesting that females grazing in that area have better the body condition than those of Areas A and B (Ferretti et al., 2015). As a consequence, chamois females allow kids to suck more frequently than in Areas A and B. Furthermore, results showed higher suckling frequency and duration in Area C in the other two areas.

Some researchers suggested that the suckling bout duration and the suckling frequency could be indicators of the quantity of milk transferred

from the mother to the kid (milk intake) (Berger, 1986; Green, 1986). Conversely, Cameron et al. (1998, 1999), through the isotope-labelling technique, suggested that these two parameters should not be used as indicators of milk intake, but they can be indicators of the amount of maternal cares and milk availability.

Combining the results of probability of suckling success, suckling frequency and duration, I suggest that maternal cares of female chamois were intense in Area C than in Areas A and B. The frequency and duration of suck bouts decreased from July to October. Kids start grazing at the end of summer and they get less dependent on their mothers which in turn have to recover the lost body reserves to survive to the winter period (Berger, 1979; Corlatti, 2009). The frequency of suckling attempts was significantly higher during summer months than in autumn ones, indicating that dependence of chamois kids from suckling decreased throughout summer-autumn, but it did not disappear. However, in the deer-free-Area (Mt. Meta), this index was lower during summer than in Areas A and B. The suckling attempt frequency could be an indicator of the kid status (satisfied kid: low suckling attempt frequency, hungry kid: high suckling attempt frequency) (Berger, 1979; Green et al., 1993; Therrien et al., 2007). Area C showed a lower value of suckling attempt rate and higher values of probability of suckling success and suck frequency, as well as suckling duration, suggesting that kids were less hungry than in other areas.

The aggression rate could be an indicator of the intraspecific competition between grazing individuals. If availability and quality of summer pastures are greater, presumably the level of intraspecific competition should be lower, thus a lower aggression rate should be expected. In Area C, the rate of aggressions from the females to kids was apparentely lower than in the other Areas which further suggests that the quality of grasslands is greater in the former than in the latter, although differences between sites were not significant.

Birth ratio was comparable across study areas, winter survival of chamois kids was the highest in Area C. Furthermore, previous studies

showed lower percentages of younger individuals in Areas A and B than in Area C, because of a higher winter mortality of kids in the former than in the latter (Latini, 2011; Ferretti et al., 2015).

These results suggested that highly nutritious grasslands (e.g. Mt. Meta) favour the foraging efficiency of chamois females and in turn, the intensity of maternal cares. In turn, higher availability of milk and more frequent/longer suck bouts during summer-early autumn, should allow chamois kids to grow better and faster and then, favouring their winter survival (Berger, 1979; Festa-Bianchet et al., 1997; Therrien et al., 2007).

Interspecific competition could be an important factor triggering the depletion of food resources, with negative effects on maternal cares, growth and survival of ungulates, but relevant published information is negligible for ungulates. High densities of ungulates could affect the vegetation cover because of grazing and trampling activities (Putman, 1986a, 1996; Hobbs, 1996). In fact, ungulates could graze selectively and frequently certain plant species, which could influence plant compositions of alpine grasslands. A higher use of these plant species could determine a reduction of their frequency and cover and an increase of unpalatable ones, with negative effects on nutritional quality of summer pasture for herbivores (Morecroft et al., 2001). Previous studies suggested that the presence of deer at high density could modify the vegetation compositions of grasslands and woody areas, because of their grazing and trampling activities (Kirby, 2001; Nagaike et al., 2012). Furthermore, the intense and constant grazing and trampling activities could determine physical damages to the vegetation cover (Lovari et al., 2014; Ferretti et al., 2015). Then, all these factors could alter the quality of summer forage of alpine grasslands, with negative effects on the conservation of other species (Cooke and Farrell, 2001).

In my study-areas, it has been shown previously that the presence of red deer at high density could affect the availability and quality of summer forage, suitable for the Apennine chamois (Ferretti et al., 2015). In fact,

grazing and trampling activities of red deer probably reduce vegetation cover and frequency on alpine grasslands where chamois also graze during summer and mid-autumn. In turn, availability of nutritious pasture for chamois decreased faster in areas grazed by deer also than in the deer-free one, from summer to autumn (Ferretti et al., 2015). Furthermore, in Area A, i.e. Val di Rose, which is located in the historic core range of Apennine chamois, Lovari et al. (2014) showed a decrease in cover and frequency of nutritous plant species, in respect to 1982-1984 (when red deer was absent from the Area). In particular, a decrease occurred of forbs belonging to patches dominated by *Trifolium thalii* and other legumes (Ferrari et al., 1988), while a contemporary increase of unpalatable plants has been reported (Lovari et al., 2014).

These results suggest that the presence of red deer at high densities affected the availability and quality of forage for Apennine chamois, during summer and early-autumn.

Red deer can be 4-5 times heavier than chamois and they can feed on different types of vegetation according to seasons (Lovari et al., 2014). Then, the effects of grazing and trampling activities of red deer are expected to be more evident rather than those of chamois (Ferretti et al., 2015).

It has been shown that the presence of red deer could affect the foraging efficiency and diet quality of chamois females, during the period of nursing and weaning (Ferretti et al., 2015). In particular, in Areas A and B, the volume of nutritious vegetation in diet of female chamois (i.e. forbs and, especially, legumes) decreased faster than it did in Area C, indicating (*i*) a faster depletion of pasture and (*ii*) lower diet quality of individuals grazing in the former sites than in the latter ones (Ferretti et al., 2015). These results suggested that differently from Area C, in Areas A and B nutritious plant species are consumed sooner by red deer, affecting the foraging efficiency of chamois females. In fact, the number of bite on grass/min (bite rate) was lower in the deer-present sites than in the deer-free one, probably because females have to increase the use of less

digestible species, which would determine a greater time required to process bites. Furthermore, the spatial fragmentation of food patches determined by deer grazing and trampling and the concurrent reduction of vegetation cover forced chamois females to increase search effort for food, thus decreasing the food intake rate (Ferretti et al., 2015). In turn, frequency and intensity of maternal cares are expected to decrease in areas grazed also by deer. Thus, my results suggested that the presence of red deer at high density could affect the availability and quality of summer pastures for chamois, with cascade, negative effects on maternal cares.

Most likely, climate change is another important factor triggering the decrease of pasture quality. Apennine chamois rely on nutritious, cold-adapted forb patches dominated by *Trifolium thalii* and other legumes (Ferrari et al., 1988). These communities are frequent in the Alps, but rare and extra-zonal in the Apennines and they are associated to terrains with long-lasting snow cover (Ferrari et al., 1988). Growing temperatures and reduction of quantity and duration of snow cover are expected to negatively influence the abundance of snowbed vegetation (e.g. *Trifolium thalii*–dominated communities, Schob et al., 2009; Gottfried et al., 2012). In turn, the quality of pasture for alpine ungulates like chamois should be affected by environmental changes.

In many mountainous areas of Europe, a phenomenon called "termophilization" has been recently described in upper grasslands, i.e. an increase of termophilous species and a concurrent decrease of cold-adapted ones (Gottfried et al., 2012; Pauli et al., 2012; Stanisci et al., 2014. In Majella National Park, an increase has been observed for emicryptophytes (perennial plant species that survive to the adverse season thanks to buds placed above ground), camephytes (perennial plant species that survive to the adverse season thanks to buds placed at most 30-40cm from the ground) and graminoid species (Stanisci et al., 2014). In my study Area A, i.e. upper Val di Rose, the only area in ALMNP where data on vegetation composition of grasslands in past decades were available, a lower frequency/cover of

nutritious plant species, including *Trifolium thalii*, has been reported in 2010-2011 in respect to 1980-1982 (Lovari et al., 2014), suggesting that climate change could have reduced the availability of nutritious pasture for chamois. Although climate change could have not yet affected chamois populations at high elevation sites, e.g. in my Area C, in the Majella National Park or in the Gran Sasso-Monti della Laga National Park, where chamois numbers have increased on the last two decades (Mari and Lovari, 2006), it could have affected pasture quality at low-altitude sites.

Secondary successions in secondary, abandoned meadows (e.g. Areas A and B: see Lovari et al., 2014 for Area A) could trigger the spread of unpalatable tall grass and reduce the total area available to grazing, further affecting pasture quality for chamois. Most likely, the action of grazing and/or trampling by red deer at high density accelerates the depletion of pasture. If so, resource exploitation by red deer could emphasize the negative effects on pasture triggered by another ecological factor: further data are required to confirm this hypothesis (Ferretti et al., 2015).

The decrease of Apennine chamois in its core distribution range has not been triggered by competition with livestock as Areas A and B are not used by livestock since *c.* 50 years (Lovari et al., 2014). Predation by wolf *Canis lupus* is likely to be moderate (Patalano and Lovari, 1993; Meriggi and Lovari, 1996; Grottoli, 2011), while that by golden eagle *Aquila chrysaetos* and brown bear *Ursus arctos marsicanus* is probably only occasional (Fico et al., 1984; Lovari, 1984; Di Domenico et al., 2012). Other potentially alternative factors can be ruled out as ultimate determinants of the recent decline of chamois (e.g. competition with other wild ungulates, roe deer *Capreolus capreolus* and wild boar *Sus scrofa*; disease; inbreeding depression; density dependence: see Lovari et al., 2014).

Several studies provided evidence of competitive interactions in ungulates in which an alien *taxon* was involved (Putman, 1996a; Forsyth and Hickling, 1998; Focardi et al., 2006; Ferretti et al., 2011a-b). Differently, Apennine chamois and red deer coexisted in the Central Apennines until the end of XIXth century and the beginning of XXth century (Tassi, 1976). During

the last few centuries, hunting, intense grazing activities of livestock in upper grasslands and wood cutting to extend these patches, modified extensively the landscape (Bonanomi et al., 2013; Lovari and Ferretti, 2013). Presently, the upper tree-line is *c.* 150 m below its previous, natural limit in most of the Apennines (Ravazzi and Aceti, 2004). In turn, the possibility that red deer access upper grasslands above 1700-2000 m a.s.l. is great (Latini, 2010; Lovari et al., 2014; Ferretti et al., 2015). Most likely, these environmental changes have determined a greater potential for competition between red deer and chamois.

My results and previous works suggested that the presence of red deer at high density limits the availability of nutritious forage for chamois, in turn affecting the foraging behaviour of chamois females during nursing and weaning (Lovari et al., 2014; Ferretti et al., 2015). Most likely, the action of red deer has emphasised the negative effects of global warming on the quality of summer pastures. Ultimately, pasture depletion leads to a worsening of body conditions of female chamois in turn, reducing maternal cares and affecting winter survival of chamois kids (Lovari et al., 2014; Ferretti et al., 2015). My results suggest that a potential for competition can be detected also between coevolved species, because of habitat changes determined by human pressure, which may further endangered threatened *taxa* (Lovari et al., 2014). The opportunity of reintroductions should be considered carefully, especially when endemic and vulnerable *taxa* are already present and could be further threatened.

CONCLUSIONS

My results suggest that resource depletion affected the diet quality of female chamois, in turn reducing frequency and intensity of maternal behaviour, ultimately leading to a decrease of winter survival of chamois kids. In turn, negative effects would show on population dynamics.

Most likely, environmental changes and interspecific competition affect the conservation status of the Apennine chamois. Climate change has modified composition of upper mountainous grasslands at the continental scale (e.g. Gottfried et al., 2012). Effects of environmental/climatic changes could be detrimental for fragile, cold-adapted nutritious plant species, which are fundamental for nutrition of chamois (Ferrari et al., 1988). Alterations of plant phenology and pasture quality could be triggered by global warming, with negative effects on availability of nutritious vegetation. Resource exploitation by red deer has further depleted pasture for chamois: grazing and/or trampling by deer are expected to reduce further the availability of nutritious vegetation for chamois (Lovari et al., 2014; Ferretti et al., 2015). In turn, the competition with red deer could emphasize locally the negative effects of global warming and act as catalyst of the local decline of chamois numbers (Lovari et al., 2014; Ferretti et al., 2015).

My findings support the hypothesis that the use of grasslands by red deer at high densities is a limiting factor for chamois: in turn, further releases of these deer to areas inhabited by Apennine chamois (or suitable to its re-introduction) should be discouraged (Lovari et al., 2014; Ferretti et al., 2015).

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